



Revisiting the relationship between common weather variables and loblolly–shortleaf pine seed crops in natural stands

MICHAEL D. CAIN and MICHAEL G. SHELTON

USDA Forest Service, Southern Research Station, P.O. Box 3516, University of Arkansas,
Monticello, AR 71656–3516, USA

(e-mail: mcain/srs_monticello@fs.fed.us)

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Abstract. Seed production was monitored during 24 years using seed-collection traps in loblolly–shortleaf pine (*Pinus taeda* L.–*P. echinata* Mill.) stands located in southeast Arkansas, north-central Louisiana, and southwest Mississippi on the southeastern Coastal Plain, USA. Sound seed production was correlated with mean monthly precipitation and temperature from National Oceanic and Atmospheric Administration weather stations located near the seed-collection areas to determine the potential of weather factors in forecasting pine seed crops. Correlations were restricted to three critical periods in the pine reproductive cycle – strobili primordia differentiation, pollination, and fertilization. The most important ($P \leq 0.05$) variables correlated with pine seed production for combined locations were cumulative precipitation ($r = +0.60$) during July, August, and September at 27 to 25 months before seed dispersal and mean temperature ($r = -0.45$) in August at 26 months before seed dispersal. Because multiple environmental factors can negatively impact pine seed development during the two years following strobili primordia differentiation, seed-production forecasts based on weather variables should be verified by on-site cone counts during the summer preceding autumn seed dispersal.

Introduction

Natural regeneration is an important method for establishing the southern pines because two-thirds of pine stands in the southeastern United States originated from natural seedfall (USDA, Forest Service 1988). However, an often-cited disadvantage for natural regeneration of southern pines is that inadequate seed crops can delay the process even when cone-bearing pines are growing on or adjacent to the site (Barnett and Baker 1991).

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Such concerns may be warranted in regions of consistently poor pine seed production, but in the Upper Coastal Plain of the West Gulf Region in the southeastern USA, loblolly pines (*Pinus taeda* L.) in managed natural stands tend to produce good seed crops during 3 out of 5 years (Cain 1991b) or 7 out of 10 years (Cain 1993). A good seed crop should produce $\geq 100,000$ sound seeds/ha to adequately regenerate an area under average conditions.

Loblolly and shortleaf pines (*Pinus echinata* Mill.) are common associates throughout most of the southeastern U.S. and are among the most important and widespread of the southern pines (Baker and Langdon 1990; Lawson 1990). As such, land managers who rely on natural reproduction cutting methods to sustain their forest stands would benefit from reliable techniques that can forecast potential seed crops some months in advance of actual seedfall.

In a survey of seed production from southern pines, Wakeley (1954) reported years of heavy seed production and years of widespread failure, with no predictable pattern. This raised the question as to whether natural pine seed crops were reliable enough for landowners to depend on for regeneration from year to year. Wenger (1957) also agreed that loblolly pine cone crops fluctuate widely, but noted that they are somewhat uniform over extensive areas during any one year. He surmised that these uniform fluctuations over broad localities suggested that weather was a major factor contributing to the success or failure of pine cone crops. If a correlation exists between pine seed crops and weather variables similar to that reported between fire and weather (Swetnam and Betancourt 1992; Yaussy and Sutherland 1994), such knowledge would be extremely useful in planning cone collections, reproduction cutting, or site preparation for natural regeneration purposes, but Wenger cautioned that one's use of prediction mechanisms requires an understanding of the basic causes of cone-crop fluctuation.

In loblolly and shortleaf pines, more than two years are needed between strobili (flower) initiation and seed maturity (Figure 1). During that time, a pine's reproductive cycle can be influenced by several chemical and physiological mechanisms: hormones, nutrients, soil moisture, light, and temperature (Barnett and Haugen 1995). Some of these mechanisms can be modified by silvicultural intervention. For example, in partially-cut pine stands, seed crops could increase because thinning would tend to enhance the vigor of retained trees, whereas seed production in isolated pines might be reduced because of inadequate pollination.

Our objectives in this paper are to review past efforts at forecasting seed crops in loblolly-shortleaf pine stands and to offer additional insights into the reliability of these techniques relative to 24 years of loblolly and shortleaf pine seed-crop data collected coincidentally in natural stands of southeast

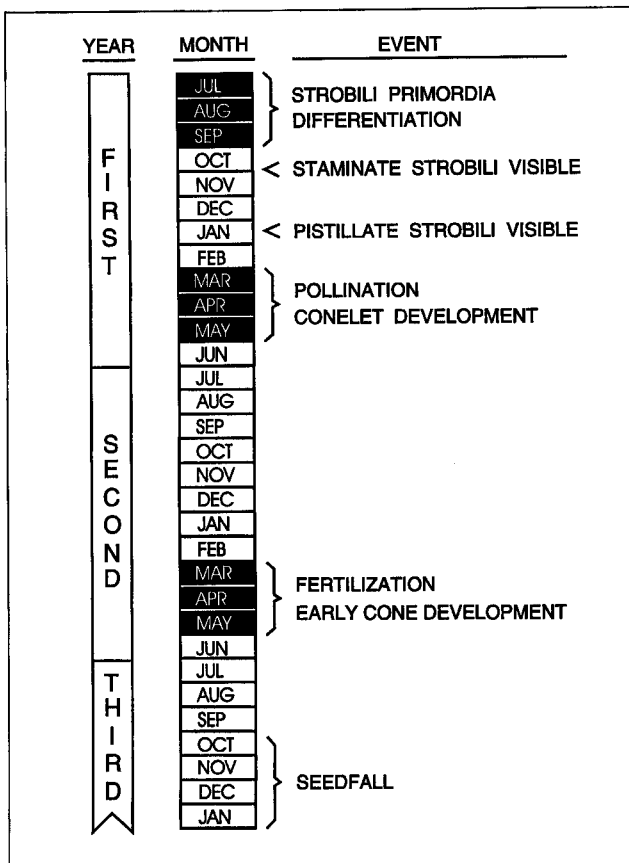


Figure 1. Loblolly and shortleaf pine reproductive cycle. Shaded areas correspond to three critical periods in the cycle – strobili primordia differentiation, pollination, and fertilization – according to Lamb et al. (1973)

Arkansas, north-central Louisiana, and southwest Mississippi. Much of the research correlating southern pine seed crops and weather variables has been restricted to seed orchards where cultural treatments (i.e., application of pesticides, irrigation, and fertilization) can be applied to mediate weather conditions. Less research has been focused on similar relationships in natural stands. As Schultz (1997) pointed out in his loblolly pine monograph: “Research needs in natural regeneration include reliable methods to predict poor seed crops before conelet development so sufficient lead time is available to stimulate flower and seed production.” Similar research needs have also been recognized for shortleaf pine (Sword and Barnett 1992). By way of this publication, the authors hope to encourage discussion and further investigation into this neglected area of research.

Methods

Study areas

Data for the present investigation were obtained from several active research studies located in the Upper Coastal Plain of southeast Arkansas (33°02' N latitude and 91°56' W longitude), north-central Louisiana (31°46' N latitude and 92°33' W longitude), and southwest Mississippi (31°21' N latitude and 91°02' W longitude) (Figure 2). Soils are Bude and Providence silt loams (Glossaquic and Typic Fragiudalfs, respectively) in Arkansas, Cadeville very fine sandy loam (Albaquic Hapludalf) in Louisiana, and Lorman silt loam (Vertic Hapludalf) in Mississippi. Although elevation ranges from 43 m in Louisiana to 70 m in Mississippi, site index at all three locations is 26–27 m for loblolly pine at base age 50 years. Mean annual precipitation ranges from 140 cm in Arkansas and Louisiana to 147 cm in Mississippi with seasonal extremes being dry autumns with wet winters and springs. Across this area, daily minimum and maximum temperatures during the growing season (March through September) average 16 and 29 °C, respectively. During the dormant season (October through February), minimum temperatures average 5 °C and maximums average 19 °C.

In Arkansas, stands were managed primarily for pine timber production using uneven-aged silvicultural techniques (principally single-tree selection), but other stand conditions included a pine seed-tree area and an unmanaged pine-hardwood forest. In Louisiana, the management strategy was to develop uneven-aged pine-hardwood stands using group selection. In Mississippi, stand management was by single-tree selection for pine timber production, but there was hardwood retention on some plots.

In single-tree selection, the objective is to produce high-quality pine sawtimber while ensuring a continuous progression of seedlings and saplings into the larger and more commercially valuable size classes. As such, the poorest quality trees are harvested during successive cutting cycles that may range from 3 to 10 years, and the best trees are retained to provide a seed source for natural regeneration while their merchantable value appreciates because of increased volume growth. These same principles apply to group selection, but openings created during cycle cuts are larger than those produced by single-tree selection.

Seed collection

For all investigations, pine seed production was monitored annually to coincide with natural seed dispersal – beginning in early October of one year and ending in early March of the next year. In Arkansas, there was a break in



Figure 2. Map showing location of study sites (■) in the Coastal Plain of Arkansas, Louisiana, and Mississippi where loblolly–shortleaf pine seed crops were monitored.

the interval during which pine seedfall was monitored. Grano (1970, 1973) monitored pine seedfall in two separate investigations. The first began with the 1964–1965 seed year and ended with the 1967–1968 seed year in an uneven-aged pine stand that had been managed for nearly 30 years using single-tree selection. Within the stand, pine seedfall was monitored on fifty-one 0.1-ha plots where pine basal areas ranged from 3 m²/ha to 21 m²/ha in trees of seed-bearing size. In the second investigation, pine seedfall was monitored around 17 loblolly pine seed trees beginning with the 1963–1964 seed year and ending with the 1969–1970 seed year. Seed trees were 41 to 53 cm in DBH (diameter at breast height, taken 1.37 m above the soil surface) and ranged from 38 to 81 years in age. For both investigations, seed-collection traps measured 0.2 m² each, with 51 seed traps in the first study and 204 seed traps in the second study. During each seed year, seed collections were made weekly. Seed soundness was determined by either a 28-day germination test or cut test. In the latter test, seeds were cut open and those containing fully developed, firm, undamaged, and healthy gametophyte tissue were judged

as potentially viable and were recorded as sound seeds (Bonner 1974). The cut test can be a reliable indicator of viability when applied to fresh seeds (Bonner et al. 1994).

The next period of pine seed collection in southeast Arkansas included 17 consecutive seed years beginning with the winter of 1980–1981 and ending with the winter of 1996–1997. We used an average of 29 seed traps per year. Between 1980–1981 and 1992–1993, seed traps measured 0.2 m² each and were monitored weekly. Beginning with the 1993–1994 seed year through the 1996–1997 seed year, seed traps measured 0.08 m² each (Cain and Shelton 1993) and were monitored monthly. All monitoring was done in uneven-aged pine stands (Baker et al. 1996) except for the last four seed years when an unmanaged pine-hardwood stand (Cain and Shelton 1994) was included along with the managed stands. Areas monitored for pine seed production were ≥ 2 ha. Seed soundness was determined by the cut test.

In the Louisiana investigation, pine seedfall was monitored within nine 0.1-ha group-selection openings using a total of 27 seed traps that measured 0.08 m² each. Pine basal area averaged 16 m²/ha in trees of seed-bearing size that surrounded the openings. Seedfall monitoring spanned four consecutive seed years: 1991–1992 through 1994–1995.

In the Mississippi investigation, pine seedfall was monitored within eighteen 0.2-ha uneven-aged pine plots averaging from 10 to 14 m²/ha in merchantable-pine basal area with up to 7 m²/ha of hardwood basal area retained on some plots. Each seed trap measured 0.08 m², and a total of 54 seedtraps were monitored annually during five consecutive seed years: 1990–1991 through 1994–1995.

For both the Louisiana and Mississippi investigations, only two seed collections were made per year – the first was after peak seedfall in early winter, and the second was in early March. After each collection, a cut test was used to determine the number of sound seeds.

Meteorological data

In southeast Arkansas, meteorological data were recorded within a 3-km radius of all stands where seedfall was monitored during 24 years. Temperature was recorded using hygrothermographs housed in National Oceanic and Atmospheric Administration (NOAA) instrument shelters and precipitation was recorded in NOAA rain gauges. Weather variables for the Louisiana and Mississippi studies were obtained from NOAA weather stations located within 19 km of each study site.

Data analysis

Sound-seed data were pooled by seed year for analysis of separate locations and combined locations. Seed production was transformed by taking the cube root, which reduced the extreme variability of the data and provided a normal distribution. Based on the Shapiro-Wilk test (SAS 1989), we failed to reject the null hypothesis of normality of the cube root of seed production ($P = 0.53$). Seed production was then correlated with mean monthly temperature ($^{\circ}\text{C}$) and precipitation (cm) occurring during three critical periods in the pine reproductive cycle (strobili primordia differentiation, pollination, and fertilization) (Figure 1). Each of these periods extended for three months (Lamb et al. 1973). This restricted our analysis to correlations between seed production and 18 weather variables (two variable types – temperature and precipitation, three critical periods, and three months within each period). We also evaluated the mean temperature and precipitation that occurred within each critical 3-month interval in the pine reproductive cycle (Figure 1). Correlations were considered statistically significant at the $\alpha = 0.10$ probability level. The number of weather variables tested was limited because the possibility of statistically significant correlations occurring by chance increases with the number of variables (Hintze 1996). In addition, an equation relating sound seed percentage to total seed production was fitted by nonlinear least squares regression using the SAS procedure MODEL (SAS 1988). For presented regression equations, examination of the residuals suggested no problems with autocorrelation that might have resulted from the time-series nature of the data.

Results

Precipitation correlations

During strobili primordia differentiation, at 25 to 27 months (July, August, and September) before seed dispersal, there was a positive correlation between pine seed production and precipitation in southeast Arkansas ($P \leq 0.01$) using the 1980 through 1996 seed crops, and in Louisiana and Mississippi ($P = 0.04$) using the 1990 through 1994 seed crops (Table 1). During the same critical period, seed-crop data taken from 1963 through 1969 in southeast Arkansas indicated a negative but nonsignificant correlation with precipitation. Yet, when all sites and years were combined, precipitation during strobili primordia differentiation exhibited another positive correlation ($P \leq 0.01$) with seed production and was the most important of all weather variables tested (Table 1).

Table 1. Correlation coefficients for relationships between sound seed production and mean weather conditions during critical periods in the loblolly and shortleaf pine reproductive cycle by locations and sampling intervals in the southeastern Coastal Plain, USA.

Three-month mean weather variables by locations ¹ and sampling intervals	Reproduction processes		
	Strobili primordia differentiation ²	Pollination ³	Fertilization ⁴
Precipitation	Correlation coefficients (probability levels)		
AR 1980–1996	0.73 (<0.01)	–0.27 (0.29)	0.38 (0.13)
AR 1963–1969	–0.42 (0.35)	–0.10 (0.83)	0.15 (0.75)
LA/MS 1990–1994	0.70 (0.04)	–0.74 (0.02)	–0.17 (0.67)
Combined	0.60 (<0.01)	–0.32 (0.07)	0.20 (0.26)
Temperature			
AR 1980–1996	–0.48 (0.05)	0.29 (0.25)	–0.16 (0.54)
AR 1963–1969	0.35 (0.44)	–0.13 (0.79)	–0.10 (0.83)
LA/MS 1990–1994	–0.40 (0.29)	–0.55 (0.13)	–0.53 (0.14)
Combined	–0.35 (0.05)	–0.09 (0.64)	–0.29 (0.10)

¹AR represents southeast Arkansas; LA/MS includes combined data from studies in north-central Louisiana and southwest Mississippi. Number of observations by location: AR 1980–96 (17), AR 1963–69 (7), LA/MS 1990–94 (9), Combined (33).

²July, August, and September, at 27 to 25 months before seed dispersal.

³March April, and May, at 19 to 17 months before seed dispersal.

⁴March, April, and May, at 7 to 5 months before seed dispersal.

Figure 3 illustrates the linear relationship ($r^2 = 0.36$, $P < 0.01$) between pine seed production (cube-root transformed) and July through September precipitation two years earlier for seed-collection intervals by locations. For seed crops in southeast Arkansas (1980–1996), Louisiana, and Mississippi, the relationships were positive (Table 1). For the 1963–1969 Arkansas data, the negative correlation (Table 1) is attributed to the narrow range in recorded cumulative precipitation (25–39 cm) and seed crops (27,000–1,000,000 seeds/ha) that occurred during that short collection interval (Figure 3). The narrow range in mean precipitation for July, August, and September from 1963–1969 was generally clustered around the 65-year historical mean of 28.5 cm for cumulative precipitation during those three months in southeast Arkansas.

During the period of pollination, at 17 to 19 months (March, April, and May) before seed dispersal, precipitation exhibited a negative correlation with pine seed production at all locations (Table 1). The negative correlations were

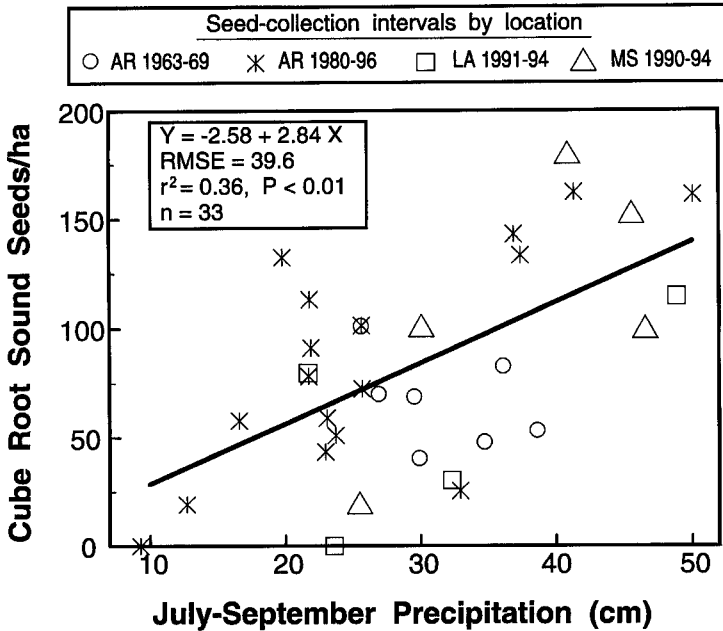


Figure 3. Relationship between cumulative precipitation during strobili primordia differentiation and loblolly-shortleaf pine seed production two years (25-27 months) later. Each point represents a yearly value for the specified location.

statistically significant at the Louisiana and Mississippi locations ($P = 0.02$) and at combined locations ($P = 0.07$). During the period of fertilization, at 7 to 5 months (March, April, and May) before seed dispersal, there were no consistent nor statistically significant correlations ($P > 0.10$) between precipitation and seed production (Table 1).

Temperature correlations

For the 1980 through 1996 pine seed crops in southeast Arkansas, strobili primordia differentiation was negatively correlated ($P = 0.05$) with mean temperature (Table 1). This negative correlation between strobili differentiation and temperature also held for combined locations ($P = 0.05$). Within that 3-month period, mean temperature in August had the best linear fit ($r^2 = 0.20, P < 0.01$) for combined locations (Figure 4).

All correlations of mean temperature within the critical period of pollination were statistically nonsignificant ($P > 0.10$) and showed no consistent pattern (Table 1). For the 17 consecutive pine seed crops (1980–1996) in southeast Arkansas, there was a positive correlation between temperature and pollination; whereas all other locations produced negative correlations.

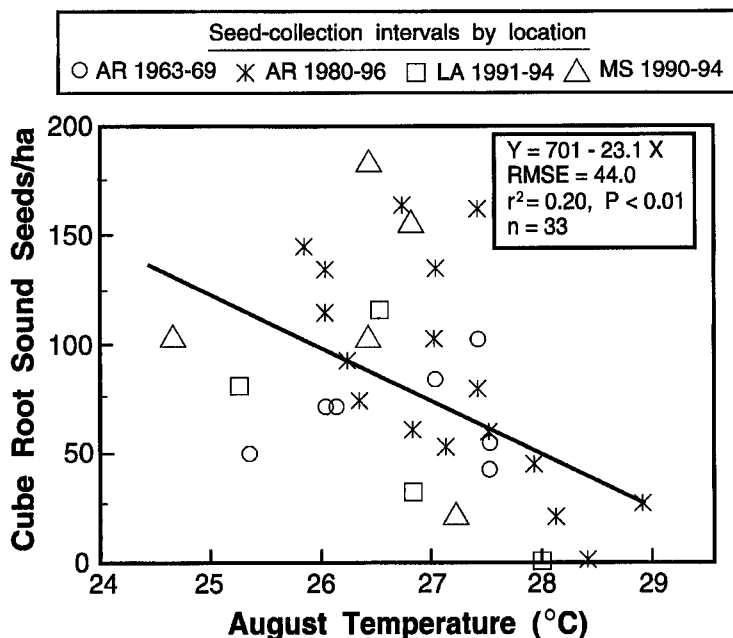


Figure 4. Relationship between mean August temperature during strobili primordia differentiation and loblolly-shortleaf pine seed production two years (26 months) later. Each point represents a yearly value for the specified location.

During the period of fertilization, mean temperature consistently exhibited negative correlations (Table 1). Yet, the only statistically significant correlation with temperature during this critical period was for combined locations ($P = 0.10$).

Pine seed dispersal and relative soundness

In the operational utilization of natural pine seed crops, both the periodicity of dispersal and the relative soundness of the seed crops are important considerations. During the 17 consecutive years (1980–1996) that pine seedfall was monitored in southeast Arkansas, seeds were collected from traps on a weekly basis during the first 13 years, eight of which produced good seed crops (i.e., 100,000 to 2,000,000 sound seeds/ha). For those eight years, peak seed dispersal occurred in early November. During bumper seed years ($> 2,000,000$ sound seeds/ha) and poor seed years ($< 100,000$ sound seeds/ha), timing of peak seed dispersal in autumn and winter was less predictable (Cain 1991b).

The percentage of sound pine seeds was well correlated with annual pine seed production across study locations in the southeastern Coastal Plain as indicated in the following equation:

$$P = 67.3 \{1 - \exp(-0.00209T)\}$$

Where P is percentage sound seeds, T is total seeds/ha in thousands, fit index (equivalent to r^2 for linear equations) is 0.74, and RMSE is 12.12. Application of this equation indicates that percentage of sound seeds is nearly zero for seed-crop failures, increases rapidly through about a million total seeds/ha, and thereafter asymptotically approaches a value of 67% for larger seed crops. This relationship between seed crop size and seed soundness is consistent with the findings of Allen and Trousdell (1961).

Regional uniformity in pine seed crops

During five consecutive years, from 1990–1994, pine seed dispersal was monitored concurrently at three locations – southeast Arkansas, north-central Louisiana, and southwest Mississippi – in the southeastern Coastal Plain of the U.S. During four of these five years, sound seed production at the Arkansas and Mississippi locations was virtually the same (Figure 5) across a distance of 200 km. Pine seed production at the Louisiana location was monitored for only four consecutive years, and this site always averaged fewer sound seeds than occurred at the other two sites. However, the generally uniform trends exhibited across this extensive area (approximately 12,000 square km) tend to corroborate Wenger's (1957) hypothesis that weather is a major factor in the annual variation of pine seed crops.

Discussion

Historical perspective on weather variables

In a study of shortleaf pine seed production, Bramlett (1968) noted that the factors responsible for annual variation in flower production appeared to be primarily climatic. Bramlett surmised that climatic influences affect flowering by regulating the normal pattern of growth and development to the point that more or less flower primordia are initiated in any given year. Based on knowledge of loblolly pine's reproductive cycle, Wenger (1957) found that, during eight years, loblolly pine seed production from natural stands in North Carolina varied directly with May-to-July rainfall two years earlier.

Dewers and Moehring (1970) investigated the relationship of soil moisture stress on initiation of ovulate primordia in a 13-year-old loblolly pine

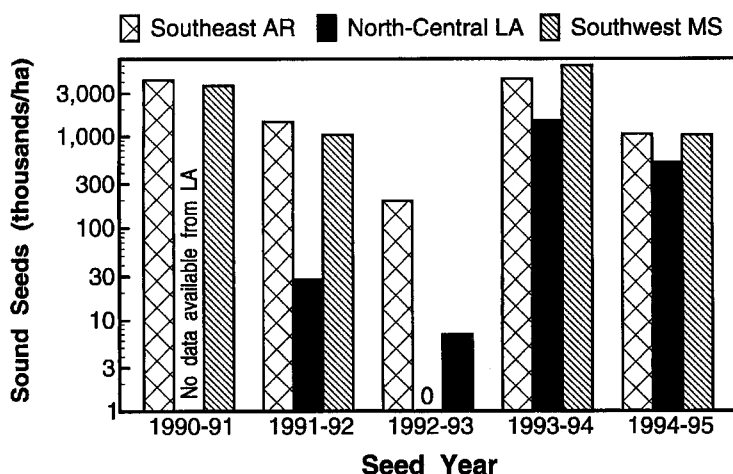


Figure 5. Variation in loblolly-shortleaf pine seed crops (logarithmic scale) during five consecutive years at three locations on the southeastern Coastal plain, USA.

seed orchard in Texas. They determined that April–June irrigation of pines followed by July–September drought improved the conelet crop one year before seed maturity. Even though their effort was restricted to a single growing season, they concluded that water stress depressed vegetative growth and promoted differentiation of reproductive tissue.

After monitoring loblolly pine seed crops for seven consecutive years in southern Arkansas, Grano (1973) reported that rainfall in the spring and summer of the year of strobili differentiation accounted for about 51% of the variation in annual production of viable seed by individual trees. Grano concluded that viable seed yields of loblolly pine were favored by a combination of abundant spring rainfall and a relatively dry summer in the year preceding flowering. Grano cited the findings of Dewers and Moehring (1970) to confirm his results. However, a reevaluation of Grano's data in combination with present results suggests that seven consecutive seed crops were insufficient to correlate with weather variables because extremes of weather and seed crops were not adequately bracketed during those seven years.

Probably the most comprehensive investigation correlating the influence of meteorological variables on seed production in loblolly pine was conducted by Lamb et al. (1973). Their work was based on 22 years of seedfall data from natural loblolly pine stands in Georgia. Weather variables included monthly precipitation, mean monthly temperature, monthly evaporation, and number of days with ≥ 0.3 cm of precipitation. These variables were then correlated with three critical periods of physiological

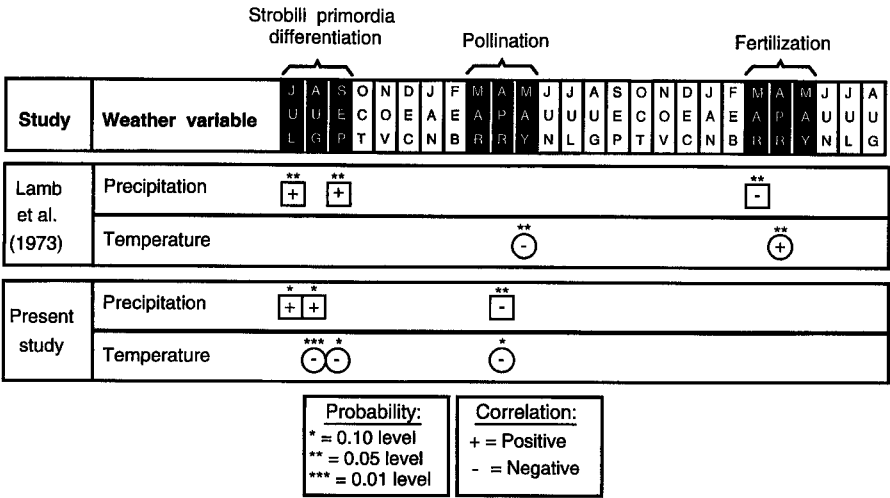


Figure 6. Correlation matrix relating monthly precipitation and temperature to seed production for loblolly and shortleaf pines. Significant correlations are shown only for critical periods of physiological activity and morphological development of loblolly pine seeds. Data are from the lower Piedmont of Georgia (Lamb et al. 1973), and the Gulf Coastal Plain of southeast Arkansas, north-central Louisiana and southwest Mississippi, USA (present study).

activity and morphological development in the pine reproductive cycle – at 27 to 25 months before seedfall when weather may affect differentiation of strobili primordia, at 19 to 17 months during pollination, and at 7 to 5 months during fertilization (Figure 6). Precipitation was an important variable in July and September of the year in which flower primordia developed. In the period of pollination, temperature and evaporation in May were found to be important variables. Lastly, during fertilization, March or April precipitation, temperature, and evaporation were important variables in loblolly pine seed production. Although the correlations by Lamb et al. (1973) were more elaborate than those of Wenger (1957), both investigations contained a common thread: adequate rainfall in spring and summer, when strobili primordia develop two years before seed maturity, tended to be well correlated with seed production in loblolly pine.

Current investigation

In the present investigation, both precipitation and temperature in the months during differentiation of strobili primordia (27 to 25 months before seed dispersal) were well correlated with sound seed production at combined locations (Figure 6). The positive correlation of pine seed production with precipitation compared favorably with findings by Wenger (1957) and Lamb

et al. (1973). These data suggest that drought conditions during this critical period of physiological activity and morphological development will have a negative effect on pine seed production two years later. Moreover, an increase in mean precipitation during the hot summer months of July, August, and September would be associated with overcast days that would reduce radiation fluxes to the ground and thereby moderate mean monthly temperatures. Consequently, there was a negative correlation between pine seed production and mean temperatures in August and September, 26 to 25 months earlier (Figure 6). Of the weather variables tested in this investigation, mean precipitation and temperature during differentiation of strobili primordia appear to have the most potential for projections of pine seed production.

Yaussy and Sutherland (1994) successfully correlated Palmer's (1965) Drought Severity Index (DSI) with area burned by wildfire one year later in the Ohio River Valley of the U.S. We initially hypothesized that drought indices might be associated with pine seed production and tested the potential of Zahner's (1956) summer water deficiency index and Palmer's DSI for correlation with pine seed production in southeast Arkansas. However, neither drought index was as well correlated with seed production as was precipitation alone. Moreover, precipitation can be more easily quantified on a particular site than complex drought indices.

According to Kuuseoks et al. (1997), factors such as topography, prevailing wind direction, and distance from large bodies of water may be more important than geographic distance affecting the relationships among on-site weather data and values from regional monitoring stations. They concluded that compared to NOAA weather stations, on-site monitoring was more important for precise estimates of precipitation than for air temperature. Therefore, correlations between precipitation and pine seed production might have been improved at the Mississippi and Louisiana locations in the present investigation if weather data had been collected on site. Nevertheless, most land managers would have to rely on NOAA weather data to forecast seed production trends at the forest level.

In our investigation of the correlation between pine seed production and common weather variables, only three critical periods in the pine reproduction cycle were tested. Step-wise regression using all possible combinations of months, temperature, and precipitation might be useful when little or nothing is known about the relationships. However, the step-wise regression process has long been considered limited (Freese 1964) because the probability of revealing nonsense correlations increases with the number of variables tested.

Autumn is generally the driest season of the year throughout the southeastern U.S. and is characterized by low relative humidity and light to

moderate north-westerly winds as dry cold fronts pass through the region. These weather conditions promote the opening of mature cones in pine crowns and enhance seed dissemination. Trends in seed dispersal for loblolly and shortleaf pines are well documented in the literature and are consistent with those reported in the present investigation. For example, an 8-year evaluation of loblolly pine seed production and dispersal in North Carolina (Jemison and Korstian 1944) indicated that seedfall peaked in early November and was 84% complete by the end of December. Other investigations of loblolly and shortleaf pine seed dispersal in North Carolina (Pomeroy and Korstian 1949; Allen and Trousdell 1961), northern Louisiana (Campbell 1967), southeast Arkansas (Grano 1971), and east Texas (Stephenson 1963) have also shown peak seedfall in November with 81%–92% completion by the end of December. Seed dispersal information is important for land managers when scheduling harvests and site preparation for establishing natural pine regeneration.

Cone counts

It is generally recognized that actual cone counts on branches of felled pines (Trousdell 1950) or in the crowns of standing pines by using binoculars (Wenger 1953; Shelton and Wittwer 1995) is the most common and perhaps most reliable method of forecasting a good or poor seed crop in specific stands of natural loblolly and shortleaf pines (Barnett and Haugen 1995). Since cones are retained on branches of these pines for several years and assuming that relative seed yield in a previous cone crop is known, any increase or decrease in the number of new cones or conelets would provide a measure of potential seed production in advance of seed dispersal. Cones from different years are distinguished by color – in late summer, maturing cones are yellow-green whereas cones from previous years are brown. Anyone attempting to forecast pine seed crops using weather variables two years before seed dispersal should verify their prediction with on-site cone counts during the summer preceding actual seedfall.

Management implications

Foresters who rely on natural reproduction cutting methods to regenerate their stands could be faced with costly regeneration failures if poor seed crops coincide with harvest cuts and cultural measures. That is because herbaceous vegetation and woody plants tend to capture good sites (site index > 26 m at 50 years for loblolly pine) within a year or two after a cut (Cain 1991a). Consequently, Trousdell (1950) proposed that a less accurate estimate of pine

seed production one year in advance of seedfall would probably be more useful to practicing foresters than one made only six months in advance.

Since the formation of mature loblolly and shortleaf pine cones spans two full growing seasons, Trousdell (1950) cautioned that nutrition, environment, age, weather, insects, animals, and possibly diseases can have a direct impact on development from buds to mature seeds. For example, Schoenike (1955) observed that heavy rains (21-cm accumulation in 4 days) coincided with peak pine pollen dissemination during mid-March in southeast Arkansas and washed tremendous quantities of pollen onto the ground just at the time of maximum receptivity for female flowers. In other examples, late-spring frosts have damaged shortleaf pine flowers in the Louisiana Coastal Plain (Campbell 1955) and the Virginia Piedmont (Hutchinson and Bramlett 1964, Bramlett 1972). Consequently, any prediction system relying on common weather variables will tend to overestimate actual seed production because such estimates cannot account for most of these deleterious influences that occur during critical stages of cone development.

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